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# Ranges of offshore decapod crustaceans in the eastern Pacific Ocean

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Abstract. Distributions of offshore decapods in the eastern Pacific fall into a pattern of at least five clusters: the Aleutian Islands to Washington, Washington or Oregon to southern California, Baja California and the Gulf of California to central America, Panama or Colombia to Peru, and Chile to Cape Horn. These clusters are supported by distributional data at all depths considered, although there is more blurring of provincial boundaries at depths greater than 1500 m than at lesser depths. There is a sharp break in faunal distributions between that of northern Baja California and all areas to the south, largely due to the replacement of species of Pandalus to the north by species of Heterocarpus to the south. The northeastern Pacific is particularly rich in species of hippolytid shrimps and lithodid crabs and contains endemic genera of the families Crangonidae and Majidae. Species in these and other groups probably underwent extensive radiation in the late Cenozoic and dispersed from the northern Pacific into the northern Atlantic and less readily into the southern hemisphere. Compared to the northeastern Pacific, the western coast of South America is poor in the total number of species and the degree of endemism in decapods. Except for a few cosmopolitan species of the lower continental slopes, North and South America have no species in common.

## INTRODUCTION

The coast of the Americas constitutes the longest continuous north—south ocean margin in the world. In shallow and intertidal regions, the distributions of co-occuring invertebrate species have been used to define at least six zoogeographic provinces. From north to south, these are the Aleutian (the Bering Sea to Puget Sound), the Oregonian (Puget Sound to Point Conception, California), the Californian (Point Conception to approximately Bahía Magdalena, Baja California, Mexico), the Panamic (Bahía Magdalena to the Gulf of Guayaquil, including the Gulf of California), the Peru—Chilean (northern Peru to approximately Isla Chiloe, Chile), and the Magellanic (Isla Chiloe to Cape Horn) (Dana 1853, Keen 1937, Ekman 1967, Valentine 1966, Briggs 1974).

Different interpretations have been offered for designations of provinces. For example, Brusca and Wallerstein (1979) referred to all of the coastal warm-water (subtropical/tropical) area as the Eastern Pacific Zoogeographic Region, noting Briggs' subdivisions of four provinces: the Cortez, Mexican, Panamic, and Galapagos. They also recognized the west coast of Baja California between Punta Eugenia and Bahía Magdalena as a broad transition zone between the Californian and Cortez provinces. Keen (1937) designated subprovinces of the Oregonian province. Garth (1955) considered the fauna of the outer coast of Baja California to belong to a province separate from that of the Gulf of California, but Briggs (1974) included both faunas in a common province. All of these interpretations were based on species living no deeper than the continental shelf.

There are very few studies of wide-scale distributional patterns of invertebrates of offshore areas, at depths of 50 m or more. Menzies *et al.* (1973) defined offshore provinces by depth, sorting invertebrate species into a Shelf Province (about 246 m or less), an Archibenthal Zone of transition (to 1000 m), and a deeper Abyssal Province. Their study did not consider distributions by latitude. However, Cutler (1975) noted that the region of Cape Lookout, North Carolina, constitutes a zoogeographical barrier to sipunculid and pogonophoran worms not only of shallow waters, but also to species living on the continental slope. Parker (1963) reported the distributions of decapods of the eastern Pacific by latitude,

but based his work strictly on published literature and made no distinction between species living inside the Gulf of California and those on the open Pacific coast.

Work on mollusks in the eastern Pacific suggests that latitudinal distribution patterns in this group change with depth. Reports by Jackson (1974) and Jablonski and Valentine (1981) indicate that species living in very shallow water tend to have broader latitudinal distributions than those living deeper on the continental shelf, but the trend in decreasing range with decreasing depth reverses itself near the shelf–slope break, below which species tend to have increasingly wider ranges. The wider latitudinal ranges of species living below the shelf break was attributed by Jackson to the damping of environmental fluctuations with greater depth. Jablonski and Valentine (1981) noted that western American molluscan provincial boundaries are well defined down to 100 m and can be detected across the continental shelf.

Data for any group of offshore invertebrates in the eastern Pacific are scanty. Decapod crustaceans, however, are reasonably well studied, identified, and collected. Being among the larger invertebrates, they can be taken with trawls, dredges, traps, and nets, as well as identified at times from bottom photographs. Hence, data for this group are more abundant than for others.

Published records of ranges of decapod crustaceans are scattered through expedition reports, monographs, systematic papers, and short notes. The earliest major deep-sea expedition to visit the eastern Pacific was that of the H.M.S. *Challenger*, which made collections in 1875 off Chile and Juan Fernandez Islands. Bate (1888) reported on many of the decapods taken during this trip. The U.S. Fisheries Steamer *Albatross* collected extensively off the Galapagos, Central America, and the coast of the United States from southern California to Alaska from 1888 to 1914. Information on decapods taken during its cruises can be found in the works of Benedict (1902), Faxon (1895), Rathbun (1904, 1918, 1925, 1930, and 1937) and Schmitt (1921).

Only two papers have attempted to describe assemblages of offshore eastern Pacific decapods quantitatively by depth. Pereyra and Alton (1972) reported on crustaceans and other invertebrates taken by trawls at 91–2103 m and grabs and dredges to 4ll m off the Columbia River. They provided charts and diagrams of the relative abundance of species at various depths and divided the invertebrate groups into an outer sublittoral assemablage (at 91–183 m), a bathyal assemblage (at 185–914 m, subdivided into an upper bathyal assemblage at 185–457 m and a lower bathyal assemblage at 457–914 m), and a bathyal–abyssal assemblage (at 917–1554 m). Wicksten (1980), using published and unpublished records of decapods taken by a variety of methods off southern California, divided the fauna into mainland and insular assemblages, providing numbers of specimens and stations per species at depths of 185 m or less, 185–923 m, and 923–1846 m.

Records and ranges of offshore decapods have been presented in works discussing the faunas of particular countries, states, or regions. Offshore species of Chile have been reported by Baez and Andrade (1979), of the Peru–Chile Trench and its vicinity by Haig (1955, 1974b), Garth and Haig (1971), and Garth (1973), of Peru by Mendez (1981), of California and western Mexico by Haig and Wicksten (1975) and Wicksten (1980, 1982a, 1987), of Oregon by Pereyra and Alton (1972) and McCauley (1972), and of British Columbia by Butler (1980) and Hart (1982). Records of species that cross the northern Pacific, ranging from Alaska to the Siberian coast, can be found in the work on fauna of the Kurile–Kamchatka Trench by Birshtein and Zarenkov (1972).

Ranges of many eastern Pacific decapods are included in wide-scale systematic works and short notes. Offshore peneids are discussed by Faxon (1895) and Mendez (1981). Information on carideans is included in works by de Man (1920), Holthuis (1971), Crosnier and Forest (1973), Wenner (1979), Wicksten (1977, 1978, 1979a,b, 1984), Wicksten and Mendez (1982, 1983, 1985), and Zarenkov (1976). Records of stenopodids are given by Goy (1980) and Wicksten (1982b). Lobster-like decapods are treated in the works of Manning (1970), Firth and Pequegnat (1971), Wicksten (1981), and Williams (1986). Anomurans are considered in notes and works by Bouvier (1896), Haig (1956, 1968, 1974a,b), Anderson and Cailliet (1974), and Ambler (1980). The works by Garth (1958 and 1973) provide information on brachyurans.

#### METHODS

Large collections of eastern Pacific decapods are maintained at the U.S. National Museum of Natural History, California Academy of Sciences, Allan Hancock Foundation (University of Southern California and Los Angeles County Museum), and Scripps Institution of Oceanography. While identifying and cataloguing specimens from these collections, I analyzed the localities and depths of collection of over 5000 specimens of offshore decapods from nearly 500 eastern Pacific stations. Previously unpublished records found while examining these collections were published in a short note (Wicksten 1987) as well as in previous papers (Wicksten, 1977, 1978, 1979a,b,c, 1980, 1981, 1982a,b, and 1984). I also accumulated records of depth distribution and ranges from the published literature.

For this study, I defined an offshore species as one for which the majority of records of occurrence are at 50 m or deeper. I considered only benthic species or those that normally can be collected on the bottom despite their limited abilities to swim. (Although the galatheid crab *Pleuroncodes planipes* can be abundant at 23–103 m off western Baja California, [Rowe, 1985], it was excluded from this study because most of the records in collections and the literature did not distinguish between specimens taken on the bottom and those cast ashore or swimming in the water column). Species from deep-sea hydrothermal vents and seeps were not included. See Jones (1985) for papers discussing the decapod faunas of these areas.

The area covered by this study is from the westernmost tip of the Aleutian Islands (excluding the Bering Sea) to Cape Horn, including the Galapagos Islands, Juan Fernandez Islands, and their immediate surroundings. The area was arbitrarily divided into 5° "squares" of latitude and longitude (Figures 1–6), numbered at 1 for the tip of the Aleutians and running to 66 at Cape Horn (including offshore banks and nearshore islands), with 67–70 assigned to the Galapagos Islands and 71–72 to the Juan Fernandez Islands. The square bounded by 25–30°N and 110–115°W (Figure 3) was arbitrarily divided into two parts so that ranges from the outer coast of Baja California (28) could be separated from those within the Gulf of California (31). Square 8 (Figure 1) is considered to contain only the Pacific side of the Alaska Peninsula.

One hundred eighty-three species of offshore decapods are reported from the eastern Pacific (Appendix 1). In this study, endemic subspecies of widespread species (*Parapagurus pilosimanus benedicti, Pontophilus gracilis occidentalis*, and *Stereomastis sculpta pacifica*) are treated as eastern Pacific species. Ranges are treated as continuous for all species: if, for example, a species is reported only from squares 1 and 10, it is considered to occur also in squares 2–9. (No disjunct amphitropical distributions are known for any offshore eastern Pacific decapods). All species are included, including those known only from single specimens.

The interested reader can find published records of exact latitude, longitude, and depth of occurrence of individual specimens by referring to the works given for each species in Appendix 1. Records of the decapods in the collections of Scripps Institution of Oceanography have been published by Luke (1977). The decapods of the Allan Hancock collections have been card-catalogued by species and partially by station or collection site, but these data have not been published or entered into a computer. Specimens at the California Academy of Sciences are being catalogued by species.

For analysis of co-occurring species, presence—absence data were used. Each species was assigned a number, then its occurrence was entered for each 5° square in its range. Initially, I experimented with three methods of determining similarity of species composition: simple matching, Jaccard's coefficient, and the method of Rogers and Tanimoto (1960). (See Sneath and Sokal [1973] for a discussion of similarity coefficients). Of the three methods, only the last produced a phenogram that seemed to show distinguishable patterns related to geography.

Using the method of Rogers and Tanimoto (1960), I compared the squares for similarity of species composition at five depth ranges: all depths, range number 1 (0–500 m), number 2 (500–1000 m), number 3 (1000–1500 m), and number 4 (1500 m and deeper). Comparisons were done by cluster analysis with the UPGMA (unweighted pair-group analysis) clustering algorithm. A phenogram of co-occurrences was produced, with a cophenetic correlation

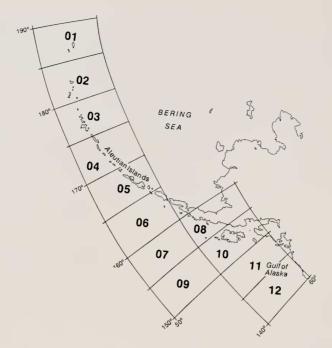


FIGURE 1. Location of  $5^{\circ} \times 5^{\circ}$  map coordinates across the North Pacific from the Aleutian Islands to the Gulf of Alaska,

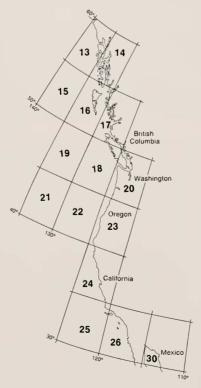


FIGURE 2. Location of  $5^{\circ} \times 5^{\circ}$  map coordinates along the west coast of North America from Alaska to Baja California Norte.

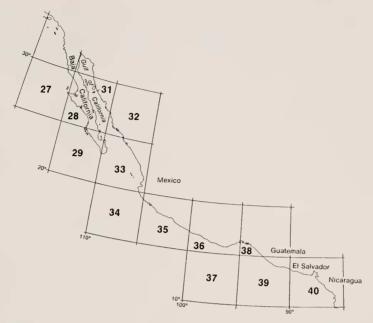


FIGURE 3. Location of  $5^{\circ} \times 5^{\circ}$  map coordinates along the west coast of Mexico and Central America. Note that numbers 28 and 31 share the same  $5^{\circ} \times 5^{\circ}$  square.

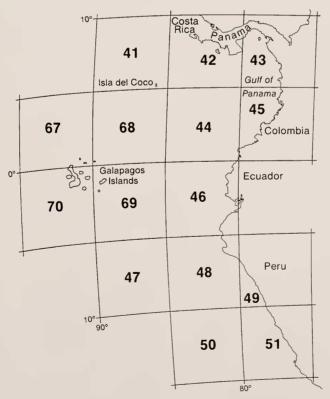


Figure 4. Location of  $5^{\circ} \times 5^{\circ}$  map coordinates from the 1sthmus of Panama to central Peru.

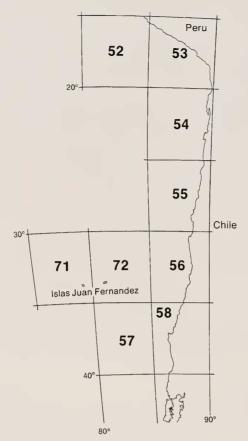


Figure 5. Location of  $5^{\circ} \times 5^{\circ}$  map coordinates from southern Peru to central Chile.

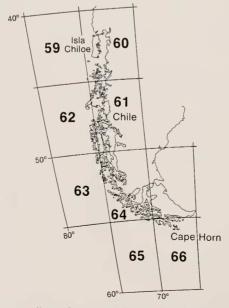


Figure 6. Location of  $5^{\circ} \times 5^{\circ}$  map coordinates from central Chile to Cape Horn.

coefficient of 0.96.

Each phenogram shows clusters of squares according to similarities. In comparing the clusters with the geography of the coast, north–south patterns appear most consistently at a similarity of approximately 0.75. Therefore, the 0.75 level of similarity was chosen arbitrarily for discussion of the clusters.

# RESULTS

Figures 7–11 are phenograms of similarities in species composition by squares. For species at all depths taken together, there are seven sets of squares at levels of similarity of 0.75 or more (Figure 7). From north to south, these include squares 1–18 and 20 (Alcutian Islands to Washington), squares 22–25 (Oregon to offshore southern California), squares 27–41 (Baja California to Isla del Coco), squares 42 and 43 (Gulf of Panama), squares 44–46 and 48–53 (Colombia to Peru), and squares 54–72 (mostly from Chile) plus the northern squares 19, 21, and 47. Square 26 (coastal southern California) constitutes a single-member group because its similarities to other squares are at levels below 0.75.

At depth range number 1 (0-500 m), there are seven clusters of squares with a similarity of 0.75 or more (Figure 8). The clusters define the following groups by geographic position: the westernmost Aleutian Islands, the Aleutians to Washington; Oregon to central California; southern California, northern Baja California, and part of the Gulf of California; the southern Gulf of California to Peru, and all others. At depth range number 2 (500–1000 m), the squares clustered at the 0.75 level follow a similar pattern (Figure 9): Aleutians to Washington, Oregon to California, square 26 alone, Baja California to Isla del Coco, Costa Rica to Ecuador, Peru, and all others. The patterns for depth ranges 3 and 4 differ slightly: at range 3 (1000–1500 m), there are eight clusters (Figure 10), and at range 4 (greater than 1500 m), there are ten (Figure 11). Those at range 3 include the following areas: the Aleutians to Washington, Oregon to California, square 26 alone, northern Baja California and part of the Gulf of California, southern Baja California to Nicaragua, Isla del Coco to Ecuador, Peru, and all others. Those at range 4 are from the Aleutians to Washington; offshore of Washington and Oregon; central and southern California; southern California, northern Baja California, and the Gulf of California; southern Baja California to Nicaragua; square 42 alone; Panama to Peru; Peru to Chile: and the rest of Chile with all remaining squares.

Regardless of the depth range considered, there is a cluster of squares that primarily represents the area off southern Chile, the Juan Fernandez Islands, and the Tufts and Cascade abyssal plains. These groupings almost surely are an artifact of the use of presence—absence data. Examination of the species composition of these squares indicates that they have almost nothing in common except for ubiquitous species such as *Parapagurus pilosimanus benedicti*.

In examining distributions at all depths, one finds taxa characteristic of particular regions. Table 1 presents examples of endemic species and species reaching either their northern or southern limits in particular regions. Refer to Appendix 1 for details of ranges and depth distributions of the species.

Comparisons of patterns of ranges at different depths reveal only slight differences. At any depth, there is a sharp break between species that range from northern Baja California northward and those that range from there southward. The area from the Aleutians to Washington seems to remain distinct in its fauna regardless of depth. At all depths, however,

patterns of clustering can be seen.

In comparing distributions of eastern Pacific offshore species with those of shallow water, one sees similar north—south changes in species composition. The Aleutian Province seems to retain its identity into deeper water. The area from Washington to central California seems to contain a mixture of more northerly and southerly ranging species. Square 26 (Point Conception to San Quintin Bay, Baja California, hereafter called the Californian Province) is distinct at all depths. This area includes marked zoogeographic boundaries for shallow-water species: Point Conception is the northern boundary of the Californian Province, while San Quintin Bay is the beginning of a region of transition between the temperate Californian Province and tropical regions to the south. The fauna of southwestern Baja California and much of the Gulf of California either forms a unit of its own or shows similarity to faunas

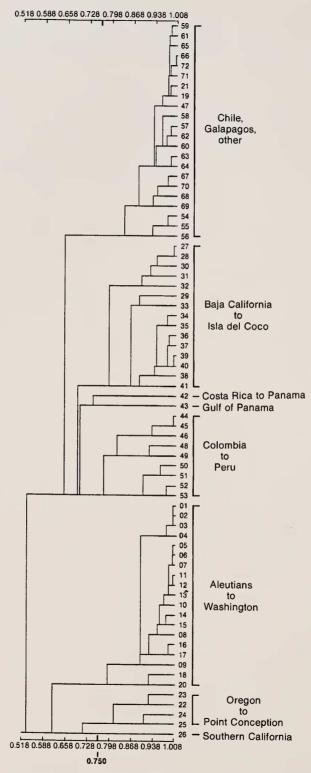


FIGURE 7. Phenogram of similarities between all squares in Figures 1–6 by presence or absence of all species at all depths. General geographic locations of the squares are given at right. Comparisons done by the methods of Rogers and Tanimoto (1960) with UPGMA cluster analysis. Clusters defined at the 0.750 level of similarity.

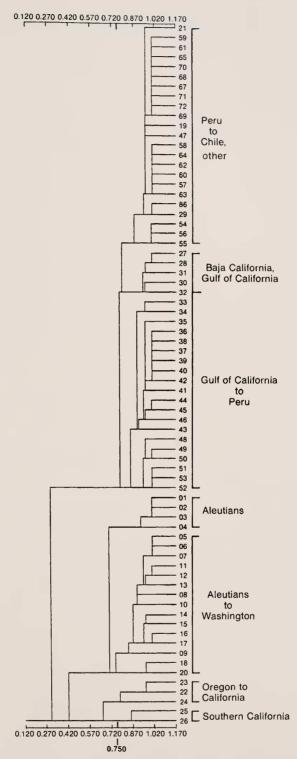


FIGURE 8. Phenogram of similarities between all squares in Figures 1–6 at depth range 1 (0–500 m). All species found at the particular depth range are used in determining similarities, including species found at other depth ranges. All squares are assumed to contain all depth ranges. Comparisons done by the methods of Rogers and Tanimoto (1960) with UPGMA cluster analysis. Clusters defined at the 0.750 level of similarity.

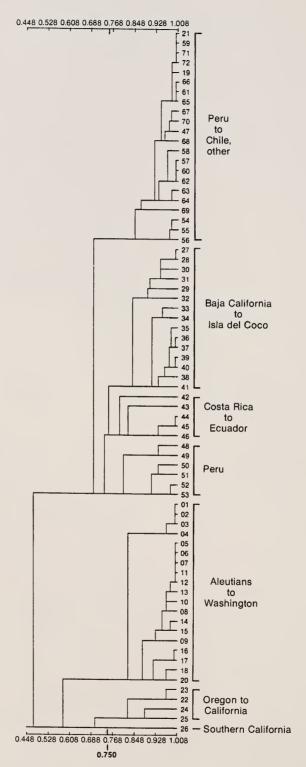


FIGURE 9. Phenogram of similarities between squares at depth range 2 (500–1000 m). All species found at the particular depth range are used in determining similarities, including species found at other depth ranges. All squares are assumed to contain all depth ranges. Comparisons done by the methods of Rogers and Tanimoto (1960) with UPGMA cluster analysis. Clusters defined at the 0.750 level of similarity.

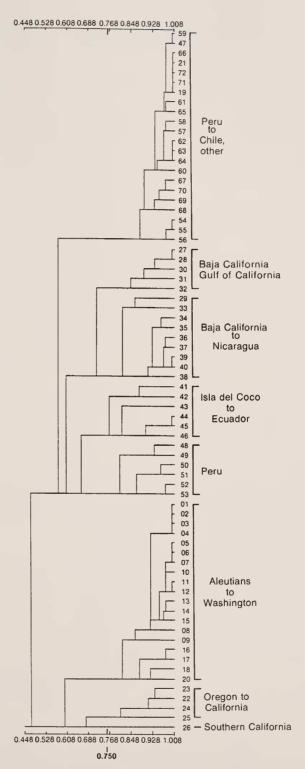


FIGURE 10. Phenogram of similarities between squares at depth range 3 (1000–1500 m). All species found at the particular depth range are used in determining similarities, including species found at other depth ranges. All squares are assumed to contain all depth ranges. Comparisons done by the methods of Rogers and Tanimoto (1960) with UPGMA cluster analysis. Clusters defined at the 0.750 level of similarity.

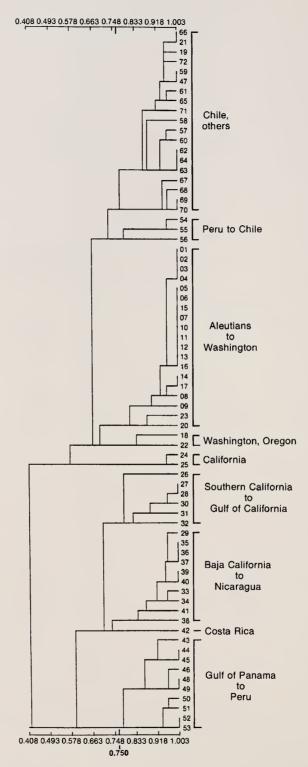


FIGURE 11. Phenogram of similarities between squares at depth range 4 (1500 m and deeper). All species found at the particular depth range are used in determining similarities, including species found at other depth ranges. All squares are assumed to contain all depth ranges. Comparisons done by the methods of Rogers and Tanimoto (1960) with UPGMA cluster analysis. Clusters defined at the 0.750 level of similarity.

# Aleutian Islands and Bering Sea to Oregon:

Endemics: Eualus biunguis, E. pusiolus, E. suckleyi, E. townsendi, Heptacarpus moseri, Pandalopsis dispar, Pandalus goniurus, P. hypsinotus, P. stenolepis, P. tridens, Argis ovifer, Pagurus confragosus, P. cornutus, Lithodes aequispina, Chirostylus sp., Munidopsis beringana, Hyas lyratus.

Northern range limits: Axiopsis spinulicauda, Calastacus stilirostris, Callianassa goniophthalma, Eualus barbatus, E. macrophthalmus, Heptacarpus flexus, Lebbeus washingtonianus, Spirontocaris holmesi, S. sica, Pandalopsis ampla, Pandalus jordani, P. platyceros, Metacrangon variabilis, Paguristes turgidus, Pagurus capillatus, P. tanneri, Lopholithodes foraminatus, Paralomis multispina, Munida quadrispina, Munidopsis quadrata, M. scabra, M. verrilli, M. verrucosus, Chorilia l. longipes, C. longipes turgida.

Southern range limits: Pandalus borealis, Pagurus aleuticus, Chionoecetes angulatus angulatus, C. bairdi, Oregonia bifurca. (Species ranging into northwestern Pacific).

Central-Southern California, Northern Baja California:

Endemics: Argis californiensis, Crangon lomae, Paralithodes californiensis, P. rathbuni, Chirostylus perarmatus, Upogebia lepta.

Northern range limits: Benthesicymus altus, B. tanneri, Stereomastis sculpta pacifica, Pontophilus gracilis occidentalis, Glyphocrangon spinulosa, G. vicaria, Parapagurus haigae, Glyptolithodes cristatipes, Galathea californiensis, Munida hispida, M. depressa, M. diomedeae, Munidopsis hystrix.

Southern range limits: Callianassa goniophthalma, Eualus barbatus, Lebbeus washingtonianus, Spirontocaris holmesi, S. sica, Pandalus jordani, P. platyceros, P. tridens, Crangon abyssorum, Metacrangon variabilis, Pagurus capillatus, P. tanneri, Paguristes turgidus, Lithodes couesi, Lopholithodes foraminatus, Paralomis multispina, P. verrilli, Munida quadrispina, Munidopsis aspera, M. verrilli, Chionoecetes tanneri, Chorilia longipes, C. longipes turgida.

West Coast of Baja California, Gulf of California:

Endemics: Processa pippinae, Munida perlata.

Northern range limits: Plesionika beebei, Heterocarpus vicarius, Metacrangon procax, Nephropsis occidentalis, Upogebia jonesi, Paralomis papillata, Munidopsis hamata.

Southern range limits: Calocaris quinqueseriatus, Lebbeus vicinus montereyensis, Pandalopsis ampla, Galathea californiensis.

Southwestern Mexico:

Endemic: Heptacarpus yaldwyni.

Northern range limits: Nematocarcinus agassizii, Heterocarpus affinis, Paracrangon areolata, Sclerocrangon atrox, Glyphocrangon alata, Munida refulgens, Ethusina faxonii, Trachycarcinus corallinus.

Southern range limits: Munidopsis depressa, M. quadrata;.

Gulf of Panama:

Endemics; Glyphocrangon sicaria, Uroptychus nitidus occidentalis, Munida grucilipes, Munidopsis agassizi, M. crinita, M. hendersoniana, M. sericea, M. tanneri, Ethusa ciliatifrons, Cympolia tuberculata.

Northern range limits: Polycheles tanneri, Heterocarpus hostilis, Lithodes panamensis, Lopholithodes diomedeae, Paralomis aspera, P. longipes, Munida propinqua, Munidopsis villosa.

Southern range limits: Upogebia jonesi, Parapagurus haigae, Munidopsis hamata.

Galapagos:

Endemics: Spongicoloides galapagensis, Chirostylus defensus, Uroptychus granulatus, Munidopsis margarita, M. ornata, Rochinia cornuta, Rochinia occidentalis.

Northern range limit: Glyphocrangon loricata.

Southern range limits: Benthesicymus altus, Polycheles tanneri, Glyphocrangon vicaria, Munida hispida, Munidopsis rostrata.

Peru:

Endemics: Bathypalaemonella delsolari, Lebbeus carinatus, L. curvirostris, L. splendidus, Pagurus imarpe, Lithodes wiracocha, Paralomis inca, Cymonomus menziesi, Homolodromia robertsi, Acanthocarpus delsolari, Trizocarcinus peruvianus.

Northern range limit: Lophorochinia parabranchia.

Southern range limits: Calastacus stilirostris, Nematocarcinus agassizii, Heterocarpus affinis, H. hostilis, H. vicarius, Plesionika beebei, P. trispinus, Metacrangon procax, Paracrangon areolata, Sclerocrangon atrox, Glyphocrangon loricata, Probeebei mirabilis, Lithodes panamensis, Lopholithodes diomedeae, Paralomis aspera, P. longipes, P. papillata, Munida propinqua, Munidopsis hystrix, M. scabra, Ethusina faxonii, Trachycarcinus corallinus.

## Southern Peru to Chile:

Endemics: Nematocarcinus proximatus, Leontocaris pacificus, Heterocarpus reedi, Polycheles chilensis, Willemoesia challengeri, W. pacifica, Lebbeus scrippsi, Pagurus delsolari, Trachycarcinus hystricosus.

Northern range limit: Pagurus forceps.

Southern range limits: Benthesicymus tanneri, Nephropsis occidentalis, Stereomastis sculpta pacifica, Pontophilus gracilis occidentalis, Glyphocrangon alata, Glyptolithodes cristatipes, Munidopsis diomedae, M. verrucosus, M. villosa, Lophorochinia parabranchia.

# Southern Chile to Cape Horn:

Endemics: Campylonotus semistriatus, Steromastis suhmi, Neolithodes diomedeae, Chirostylus milneedwardsi, Munida curvipes, Munidopsis opalescens, M. trifida.

Southern range limits: Haliporoides diomedeae, Pagurus forceps, Munidopsis aspera.

farther south. From western Mexico to Peru, species appear to have greater latitudinal range in shallow water than in deeper water. The fauna of the Galapagos Islands does not appear distinct from that of the coast of tropical western America, but this may be an artifact of limited sampling: *Munidopsis margarita* and *M. ornata*, for example, are known only from specimens taken by the *Albatross* in 1891 (Faxon 1895).

Two genera of spot prawns (family Pandalidae) show allopatric distributions in the eastern Pacific. In the northeastern Pacific, species of the shrimp *Pandalus* range from Alaska to northern Baja California. From the Gulf of California south to Chile, species of *Heterocarpus* are found. Both are relatively large epibenthic shrimp of sand, mud, or gravel bottoms. Being easily recognized to genus and of commercial importance, these shrimp have been studied better than have many other decapods. The allopatric distributional pattern, therefore, is not likely to be an artifact of sampling or data analysis.

Only 25 decapod species have been reported exclusively from 1500 m or deeper in the eastern Pacific (Table 2). Of the species living at depths of 500 m or deeper, widespread; the hermit crab Parapagurus pilosimanus benedicti seems to be ubiquitous at its depth range (414–2200 m), being reported from the Kurile Islands south to the Juan Fernandez Islands (Birshtein and Zarenkov 1972, Haig 1955). Pontophilus gracilis occidentalis, Benthesicymus tanneri, Stereomastis sculpta pacifica, and Glyptolithodes cristatipes range from southern California to Chile (Wicksten 1976, 1979b, 1982, Mendez 1981). Glyphocrangon vicaria ranges from southern California to the Galapagos; G. spinulosa, from southern California to the Gulf of Panama (Wicksten 1979a). Benthesicymus altus is widespread in the Atlantic and Pacific (Schmitt 1921). Pandalopsis ampla ranges in the eastern Pacific from Washington state to the Gulf of California (Schmitt 1921, Wicksten 1987), but also has been reported in the southern Atlantic off Argentina and Uruguay (Takeda and Hatanaka 1984). Takeda and Hatanaka (1984) suspected that the Atlantic and Pacific populations may in fact be separate species. Munidopsis latirostris and Axius acutifrons range from the eastern Pacific into the Indo-West Pacific, while Munidopsis bairdii, M. ciliata, M. subsquamosa, Stereomastis nana, Nematocarcinus ensifer, Parapagurus abyssorum and Ethusina robusta are reported to be cosmopolitan at their respective depth ranges (Faxon 1895, Firth and Pequegnat 1971, Ambler 1980).

# DISCUSSION

In interpreting patterns of ranges of offshore decapods, one should bear in mind the limitations of the data base. Data for many groups of offshore crustaceans are frustratingly sparse. Sixty of the species here analyzed are known from five or fewer specimens, many collected only once at the type locality. Species living on hard bottoms, such as members of the families Stenopodidae and Chirostylidae, are difficult to collect. Other seemingly

TABLE 2. Species found at 1500 m and deeper.

Polycheles chilensis Sund: 2500 m. Stereomastis nana (Smith): 1544–2412 m. Willemoesia challengeri Sund: 2520–4000 m.

Willemoesia pacifica Sund: 2520 m.

Nematocarcinus proximatus Bate: 2516-2654 m.

Lebbeus carinatus Zarenkov: 1850 m.

Lebbeus curvirostris Zarenkov: 1680–1860 m.

Pontophilus gracilis occidentalis Faxon: 1789-4082 m.

Glyphocrangon rimapes Bate: 2500 m.

Neolithodes diomedeae (Benedict): 1923-2478 m.

Munida curvipes Benedict: 1924 m. Munida perlata Benedict: 1920–3292 m.

Munidopsis antoni (Milne Edwards): 2519–3676 m. Munidopsis aries (Milne Edwards): 2912–3025 m.

Munidopsis beringana Benedict: 2800–3276 m. Munidopsis cascadia Ambler: 2743–2926 m. Munidopsis ciliata Wood-Mason: 2030–2875 m. Munidopsis hendersoniana Faxon: 1869 m.

Munidopsis rostrata (Milne Edwards): 2153-2492 m.

Munidopsis tuftsi Ambler: 3500-3858 m.

*Munidopsis verrucosus* Khodkina: 3932–4880 m. *Munidopsis vicina* Faxon: 3063–3885 m.

Munidopsis yaquinensis Ambler: 2763–2377 m. Ethusina faxonii Rathbun: 2999–4081 m.

Ethusina faxonii Ralhbun: 2999–4081 m. Ethusina robusta (Miers): 1618–3334 m.

widespread families, such as the armored shrimps (Glyphocrangonidae) and blind lobsters (Polychelidae) live only on the lower slope at depths (1000 m or more) that have not been sampled in many areas. (There are no published reports of either family, for example, north of Point Conception, yet both probably occur along the northern Pacific slope—related species so occur in the North Atlantic and off northern Japan). Many species from off Central America, the Galapagos, and the Juan Fernandez Islands are known only from the collections of the *Albatross* and *Challenger*, not having been collected since then. It can be difficult to judge from only a few records whether or not an offshore species has a continuous or discontinuous distribution. (The lack of any amphitropical distributions among deeper decapods, for example, may be an artifact of sampling.) However, data for commercial species, such as species of *Pandalus*, are more abundant than for other decapods and may bias the analysis. Records may be misleadingly abundant in well-studied areas such as the Californian Province, where the University of California, Santa Barbara, the University of Southern California, and Scripps Institution of Oceanography are studying the benthic fauna.

If deeper waters contain a more homogeneous environment than those of the continental shelf, why can one see clusters of squares by latitude at all depth ranges? Topographic barriers, such as the trenches off Central America, Peru, and Chile and the basins and ridges of southern California may limit some benthic species, while subsurface regimes of temperature, salinity, and oxygen may limit others. Biological factors, either current or past, may be involved—little is known about dispersal abilities, predator—prey relationships, or competitive interactions of offshore decapods.

The abundance of lithodid crabs and hippolytid shrimps in the northeastern Pacific suggests that there has been evolutionary radiation of species in the area. Ekman (1967) speculated that elements of the North Atlantic fauna were derived from the North Pacific through "temporary and difficult communication." Menzies *et al.* (1973) accounted for amphiboreal distributions by dispersal of species during a Pliocene trans-Arctic sea connection between the Pacific and Atlantic. During this connection, groups previously endemic to the Pacific colonized the Atlantic. Colonization ended during the unstable glacial conditions of the Pleistocene. Such a faunal exchange across the Arctic enabled species of certain genera (such as *Spirontocaris*) to colonize the Atlantic, while others (such as species of *Heptacarpus*)

were unable to cross the "filter bridge."

Ekman (1967) noted the abundance of cold-water caridean shrimps of the family Hippolytidae in the northern Pacific, referring to these shrimps as various species of *Spirontocaris*. Holthuis (1947) split the genus into four genera, *Spirontocaris* sensu stricto, *Heptacarpus*, *Eualus*, and *Lebbeus*. Ekman's observation still has merit—species of *Spirontocaris* are far more abundant in the northern Pacific than in the northern Atlantic, the only other place where they occur. Species of *Heptacarpus* are confined to the northern Pacific, from Japan across the Aleutians to off Oaxaca, southern Mexico. More species of *Eualus* and *Lebbeus* are known from the northern Pacific than from anywhere else, although species of each occur off western South America and elsewhere; species of *Lebbeus* also occur at bathyal depths in the Indo-Pacific, the Arctic, and boreal Atlantic, while species of *Eualus* live off Europe and South Africa (Holthuis 1947, Noel 1978, Wicksten 1979c, 1984, Mendez 1981, Wicksten and Mendez 1982).

A cladistic analysis of the Hippolytidae by Christoffersen (1987) indicates that members of *Lebbeus*, *Heptacarpus*, *Spirontocaris*, *Eualus*, and the mostly tropical genera *Thor*, *Thoralus*, and *Birulia* are closely related and perhaps should be split off from the old family Hippolytidae into a new family, the Thoridae. Distributional patterns of these genera suggest origin and radiation in the Pacific with subsequent spread into the Atlantic. The patterns of distribution of the four cold-water genera resemble that of the rock crabs, genus *Cancer*, which are most abundant in the Pacific but also occur across the northern Atlantic Ocean. The patterns differ, however, in the lack of any records of the four hippolytid genera from Australia and New Zealand, where one species of *Cancer* occurs. Fossils of *Cancer* spp. suggest that these crabs originated at latest in the Miocene in the northern Pacific and dispersed from there, following cold-water regimes, in the Pliocene and Pleistocene (Nations 1975). Although there are no fossils to provide evidence of past distributions of the hippolytids, at least the four coldwater genera seem to follow much the same pattern as the species of *Cancer*.

Bouvier (1896) noted that there are many species of the king crab family (Lithodidae) in the northern Pacific: there are more in the area from the Aleutian Islands to northwestern Baja California, from the intertidal zone to bathyal depths, than elsewhere. Of those found elsewhere, species of *Lithodes* and *Paralomis* live offshore in both the northern and southern hemispheres. *Glyptolithodes cristatipes* ranges from Chile to southern California.

In two other decapod families there are genera endemic to offshore waters of the northern hemisphere. Among the bay shrimps (family Crangonidae), the genera *Argis*, *Crangon*, and *Metacrangon* live in the North Atlantic and Pacific. Of the spider crabs (Majidae), species of *Chionecetes* and *Hyas* live in the North Atlantic and Pacific, while species of *Chorilia* and *Oregonia* are found only in the northern Pacific. One majid genus, *Lophorochinia*, seems to be endemic to the Peru–Chile Trench (Garth and Haig 1971).

Decapods are not the only organisms showing relatively high diversity of species or endemism of genera in the northern Pacific. The west coast of North America is second only to Australia and New Zealand in numbers of unique algal species and is noted for such large endemic genera of brown algae as Nereocystis and Postelsia (Abbott and Hollenberg 1976). Estes and Steinberg (1987) hypothesized that the larger algae of the order Laminariales radiated in the northern Pacific following the onset of late Cenozoic polar cooling. These characteristic cold-water plants are not found in tropical regions and cannot tolerate warm ocean water. Evidence from molluscan fossils and other material suggests that the polar cooling trend could have begun in the middle to late Miocene, allowing spreading of coldwater groups. The kelps apparently spread across the northern hemisphere into the Atlantic, then later colonized the southern hemisphere after closure of the Panamic seaway halted the westward flow of warm water from the Caribbean region into the eastern Pacific. Kelps may have spread into the southern hemisphere as late as the Pleistocene, when glacial periods narrowed the distance between cold-water regions of the northern and southern hemispheres. Northern Pacific decapods may have followed a similar pattern of diversification and dispersal, but could have spread more easily than algae because of their ability to survive in cold water at greater depths. Kelps require sunlight for photosynthesis and cannot survive at depths of 50 m or more. Decapods may have spread by equatorial submergence—remaining in the same temperature regimes in the tropics as in temperate regions by moving into deeper water.

The northern Pacific contains many other examples of species-rich cold-water groups. Of the living species of chitons (Mollusca: Polyplacophora), more can be found along the northwestern coast of North America than on any other coast of comparable length in the world. Conspicuous species such as Cryptochiton stelleri and Katherina tunicata have wide ranges in the northern Pacific (Haderlie and Abbott 1980). Two families of fishes, the Embiotocidae and Hexagrammidae, are found only in the northern Pacific, from Japan to western Mexico, while species of the families Stichaeidae and Cottidae as well as of the genus Sebastodes (family Scorpaenidae), although also occurring in the northern Atlantic, are by far more diverse in the northern Pacific (Herald 1961).

Except for the examples given in the families Pandalidae, Hippolytidae, Crangonidae, Lithodidae, and Maiidae, offshore decapods of the eastern Pacific belong to widespread genera found at characteristic depths or temperatures. Menzies et al. (1973) refer to these widespread groups as the Tethyan fauna, implying that their distributions could be related to the Tethyan Seaway of tropical regions in the early Mesozoic. Latitudinal ranges of the species vary from extensive to seemingly small, but the paucity of data for many groups makes family-by-family comparison of ranges difficult.

Manning and Reaka (1987) related differences in rates of evolutionary change of stomatopod crustaceans to differences in larval dispersal ability, habitat, and body size in different lineages. Evolutionary changes in stomatopods generally are inversely related to the size of the postlarvae. Lineages of small body size seem to have the most rapid rates of evolutionary change. The degree of species endemism is associated with substrate type, speciation being seemingly more common for species inhabiting coarse rather than level bottom habitats. Larger species of temperate habitats tend to have broad ranges: for example, Hemisquilla ensigera can be found in California, Chile, New Zealand, and Australia.

Because of the scarcity of information on the distributions, habitats, and life histories of offshore decapods, it is difficult to compare their evolutionary rates to those of stomatopods. Stomatopods are rare in cold deep water, being represented by only a few species. As a general rule, small decapods seem to be more common and diverse in shallow rather than deep waters; most offshore decapods measure at least 1 cm in largest dimension. Decapods of deeper hard substrates are rarely collected, so the degree of species endemism among them is difficult to determine.

It is interesting that among eastern Pacific decapods living at 50-1500 m, there are no examples of strictly amphitropical (occurring in both northern and southern temperate regions but not in the tropics) genera or species. Some of the typically cold-water families and genera live at greater depths in tropical regions than in temperate and boreal areas—species of Lebbeus, for example, can be found almost in the intertidal zone in California, but tropical representatives of the genus are found on the continental slopes or deeper.

The fauna of western South America has fewer species and genera of decapods than does North America and has only one reported offshore endemic genus (Lophorochinia). While many of the species found from Peru south to Chile are endemic to the area, they belong to

genera with widespread distributions.

The relative paucity of offshore decapods off western South America, in both numbers of species and degree of species endemism, is difficult to explain. The coast is geologically active, but so is that of western North and Central America. It is possible that gradual cooling of the coastal waters since the Mesozoic eliminated many elements of the fauna over time: Menzies et al. (1973) noted that cooling, which extended from the Mesozoic until glaciation in the Miocene, resulted in a progressive loss of invertebrate groups from the Antarctic. Tropical waters to the north may have inhibited colonization by the common cold-water families of the northeastern Pacific. Members of genera that inhabit bathyal zones (such as Lebbeus and Lithodes) seem more likely to co-occur in the northern and southern Pacific than do groups that live in shallower areas. The slope region off Peru and Chile, however, contains extensive areas of low oxygen concentrations, inhabited by bacterial mats and not by larger invertebrates (Rowe and Haedrich 1979). Perhaps a combination of historical elimination or decrease in faunal diversity and modern conditions that inhibit decapod life has resulted in the paucity of species in this area relative to the coast of North America.

Between the fauna of the eastern Pacific and that of other offshore regions there are puzzling differences. The northern Pacific is rich in cold-water caridean shrimps of the families Pandalidae and Hippolytidae. Crabs of the family Lithodidae are more diverse than in other areas. However, the abundant red crabs, *Geryon* spp., found on the slopes of the Atlantic and Indo-West Pacific region, are entirely absent, while members of the family Goneplacidae, widespread in the warmer parts of the Atlantic, seem to be relatively uncommon on eastern Pacific slopes. No species of antlered crabs, family Latreilliidae, have been reported from the eastern Pacific, although they occur in the Atlantic, Indo-West Pacific, and Mediterranean. Giant isopods (*Bathynomus* spp.), conspicuous inhabitants of the continental slopes of the tropical western Atlantic and Indo-Pacific regions, also are absent from the eastern Pacific.

Reaka and Manning (1987) noted gaps in the distributions of otherwise worldwide groups of stomatopods. For example, the species of *Alima*, are found in tropical waters worldwide except in the eastern Pacific. They speculated that such groups have undergone extinction. Such apparent extinctions in stomatopods have been more numerous in the eastern Pacific than in the western Atlantic. Perhaps such local extinctions have occurred in decapods as well as stomatopods.

The sharp break seen at all depths between the fauna of southern California and northern Baja California combined and all areas to the south is due largely to the allopatry of *Pandalus* and *Heterocarpus*. Changes in the species composition within the family Hippolytidae also contribute to the break.

Systematic treatments of eastern Pacific decapods for the most part have considered intertidal and shallow-water species, not animals living at depths of 50 m or more. Much of the information on offshore species consists of basic descriptions and accounts of where specimens were collected without comparison of records of related species. More analysis of the evolutionary relationships of the taxa might shed light on the historical biogeography of the eastern Pacific.

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# LITERATURE CITED

- Abbott, I. A., and G.J. Hollenberg. 1976. Marine Algae of California. Stanford University Press, Stanford, California.
- Ambler, J. W. 1980. Species of Munidopsis (Crustacea, Galatheidae) occurring off Oregon and in adjacent waters. U.S. Department of the Interior Fishery Bulletin 78:13–34.
- Anderson, M. E., and G. M. Cailliet. 1974. Coastwatch: California. Underwater Naturalist 8:29-31.
- Baez, P., and H. Andrade. 1979. Crustaceos decapodos arquibentonicos frecuentes frente a la costa de Chile central. Anales del Museo de Historia Natural Valparaiso 12:219-231.
- Bate, C. S. 1888. Report on the Crustacea Macrura collected by H.M.S. *Challenger* during the years 1873–1876. Reports of the Voyage of H.M.S. *Challenger* Zoology, Vol. 24.
- Benedict, J. E. 1894. Descriptions of new genera and species of crabs of the family Lithodidae, with notes on the young of *Lithodes camtschaticus* and *Lithodes brevipes*. Proceedings of the United

- States National Museum 17:479-488.
- . 1902. Descriptions of a new genus and fortysix new species of crustaceans of the family Galatheidae, with a list of the known marine species. Proceedings of the United States National Museum 26:243–334.
- Birshtein, Y. A., and N. A. Zarenkov. 1972. Bottom decapods (Crustacea Decapoda) of the Kurile–Kamchatka Trench area. Pp. 439–447 in V. G. Bogorov (ed.) Fauna of the Kurile–Kamchatka Trench and Its Environment. Akademiya Nauk SSSR—Trudy Instituta Okeanologii Vol. 86. Israel Program for Scientific Translations, Jerusalem.
- Bouvier, E. L. 1896. Sur la classification des Lithodines et sur leur distribution dans les océans. Annales des Sciences Naturelles 8:1–46.
- Briggs, J. C. 1974. Marine Zoogeography. McGraw-Hill, New York.
- Brusca, R. C., and B. R. Wallerstein. 1979. Zoogeographic patterns of idoteid isopods in the northeast Pacific, with a review of shallow water zoogeography of the area. Bulletin of the

Biological Society of Washington 3:67-105.

Butler, T. H. 1980. Shrimps of the Pacific coast of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences 202.

Chace, F. A. Jr. 1984. The caridean shrimps (Crustacea: Decapoda) of the Albatross Philippine Expedition, 1907–1910, Part 2: Families Glyphocrangonidae and Crangonidae. Smithsonian Contributions to Zoology 397.

Christoffersen, M. L. 1987. Phylogenetic relationships of hippolytid genera, with an assignment of new families for the Crangonoidea and Alpheoidea (Crustacea, Decapoda, Caridea). Cladistics

3:348-362.

Crosnier, A., and J. Forest. 1973. Les crevettes profondes de l'Atlantique oriental tropical. Faune tropicale. X1X. Office de la Recherche Scientifique et Technique Outre-Mer, Paris.

Cutler, E. B. 1975. Zoogeographical barrier on the continental slope off Cape Lookout, North Carolina. Deep-Sea Research 22:893-901.

Dana, J. D. 1853. On the geographical distribution of Crustacea. *In* United States exploring expedition during the years 1838–1842, under the command of Charles Wilkes, U.S.N. Vol. 14, No. 2. Crustacea, pp. 696–805.

Ekman, S. 1967. Zoogeography of the Sea. Sidgwick

and Jackson, London.

Estes, J. A., and P. D. Steinberg. 1987. Predation, herbivory and kelp evolution. Paleobiology 14:19–36.

Faxon, W. 1895. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross" during 1891, Lieut. Commander Z. L. Tanner, U.S.N., commanding. 15. The stalk- eyed Crustacea. Harvard University Museum of Comparative Zoology Memoir 18.

Firth, R. W. Jr., and W. E. Pequegnat. 1971. Deep-sea lobsters of the families Polychelidae and Nephropidae (Crustacea, Decapoda) in the Gulf of Mexico and Caribbean Sea. Texas A&M University Department of Oceanography, A&M

Project 700-15 Reference 71-11T.

Garth, J. S. 1955. The case for a warm-temperate marine fauna on the west coast of North America. Pp. 19–27 *in* Essays in Natural Sciences in Honor of Captain Allan Hancock. University of Southern California Press, Los Angeles.

—. 1958. Brachyura of the Pacific coast of America: Oxyrhyncha. Allan Hancock Pacific

Expeditions Vol. 21, Part 1.

——. 1973. New taxa of brachyuran crabs from deep water off western Peru and Costa Rica. Bulletin of the Southern California Academy of Sciences 72:1–12.

——, and J. Haig. 1971. Decapod Crustacea (Anomura and Brachyura) of the Peru-Chile Trench. Anton Bruun Report 6:6.3-6.20.

Goy, J. W. 1980. Spongicoloides galapagenis, a new shrimp representing the first record of the genus from the Pacific Ocean (Crustacea: Decapoda: Stenopodidea). Proceedings of the Biological Society of Washington 93:760–770.

Haderlie, E. C., and D. P. Abbott. 1980. Polyplacophora:

The chitons. Pp. 412–428 in R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Intertidal Invertebrates of California. Stanford University Press, Stanford, California.

Haig, J. 1955. The Crustacea Anomura of Chile.
Reports of the Lund University Chile Expedition 1948–49. No. 20. Lunds Universitets Arsskrift N.
F. Avd. 2, Bd. 51, No. 12.

——. 1956. Notes on two anomuran crustaceans new to California waters. Bulletin of the Southern California Academy of Sciences 55:79–81.

—. 1968. First report of the crab family Chirostylidae of California, and description of a new species of *Chirostylus*. California Fish and Game 54:270–277.

——. 1974a. Observations on the lithodid crabs of Peru, with description of two new species. Bulletin of the Southern California Academy of Sciences 73:152–164.

——. 1974b. Two new species of *Pagurus* from deep water off Peru and Chile (Decapoda, Anomura, Paguridae). Crustaceana 27:119–130.

—, and M. K. Wicksten. 1975. First records and range extensions of crabs in California waters. Bulletin of the Southern California Academy of Sciences 74:100–104.

Hart, J. F. L. 1982. Crabs and their relatives of British Columbia. British Columbia Provincial Museum Handbook 40.

Herald, E. S. 1961. Living Fishes of the World. Doubleday, New York.

Holthuis, L. B. 1947. The Decapoda of the Siboga Expedition. Part 10. The Hippolytidae and Rhynchocinetidae. Siboga Expeditie 39a8.

——, 1971. The Atlantic shrimps of the deep-sea genus Glyphocrangon A. Milne Edwards, 1881. Bulletin of Marine Science 21:267–373.

Jablonski, D., and J. W. Valentine. 1981. Onshore-offshore gradients in recent eastern Pacific shelf faunas and their paleobiogeographic significance. In G. E. E. Seudder and J. C. Reveal (eds.). Evolution Today. Proceedings of the Second International Congress of Systematic and Evolutionary Biology, pp. 441–453.

Jackson, J. B. C. 1974. Biogeographic consequences of eurytopy and stenotopy among marine bivalves and their evolutionary significance. American Naturalist 108:541–560.

Naturalist 108:541–560

Jones, M. L. (ed.). 1985. Hydrothermal vents of the eastern Pacific: an overview. Bulletin of the Biological Society of Washington 6.

Keen, A. M. 1937. An Abridged Check List and Bibliography of West North American Marine Mollusca. Stanford University Press, Stanford, California.

Khodkina, I. V. 1973. New species of the genus Munidopsis (Decapoda, Anomura) from the east Pacific. Zoologicheskii Zhurnal 52:1156–1167.

Luke, S. R. 1977. Catalog of the benthic invertebrate collections. I. Decapod Crustacea and Stomatopoda. Scripps Institution of Oceanography Reference No. 77-9.

McCauley,, J. E. 1972. A preliminary checklist of selected groups of invertebrates from otter-trawl and dredge collections off Oregon. Pp. 409–443 in A. T. Pruter and D. L. Alverson (eds.). The Columbia River Estuary and Adjacent Ocean

Waters. Bioenvironmental Studies. University of Washington Press, Seattle.

de Man, J. G. 1920. The Decapoda of the Siboga Expedition. Part IV. Families Pasiphaeidae, Stylodactylidae, Hoplophoridae, Nematocarcinidae, Thalassocaridae, Pandalidae, Psalidopodidae, Gnathophyllidae, Processidae, Glyphocrangonidae, and Crangonidae. Siboga Expeditie 39a3.

Manning, R. B. 1970. Notes on the west American nephropidean lobster Nephrops occidentalis Faxon. Proceedings of the Biological Society of

Washington 82:865-870.

Mendez, M. 1981. Claves de identificación y distribucion de los langostinos y camarones (Crustacea: Decapoda) del mar y rios de la costa del Peru. Instituto del Mar del Peru Boletin 5.

Menzies, R. J., R. Y. George, and G. T. Rowe. 1973. Abyssal Environment and Ecology of World Oceans. Wiley, New York.

Nations, J. D. 1975. The genus Cancer (Crustacea: Brachyura): Systematics, biogeography and fossil record. Los Angeles County Natural History Museum Science Bulletin 23.

Noel, P. 1978. Eualus drachi nov. sp. (Crustacea, Caridea, Hippolytidae) des côtes françaises de la Méditerranee. Archives de Zoologie Experimentale et Générale 119:21-28.

Parker, R. H. 1963. Zoogeography and ecology of macro-invertebrates, particularly mollusks, in the Gulf of California and the continental slope off Mexico. Videnskabelige Meddelser fra Dansk Naturhistorisk Forening i Kobenhavn 126:1-1178.

Pereyra, W. T., and M. S. Alton. 1972. Distribution and relative abundance of invertebrates off the northern Oregon coast. Pp. 444-474 in A. T. Pruter and D. L. Alverson (eds.). The Columbia River Estuary and Adjacent Ocean Waters. Bioenvironmental Studies. University of Washington Press, Seattle.

Rathbun, M. J. 1904. Decapod crustaceans of the northwest coast of North America. Harriman

Alaska Expedition Report 10:1-210.

1918. The grapsoid crabs of America. Bulletin of the United States National Museum 97. 1925. The spider crabs of America. Bulletin of the United States National Museum 129.

-. 1930. The cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae, and Xanthidae. Bulletin of the United States National Museum 152.

 1937. The oxystomatous and allied crabs of America. Bulletin of the United States National Museum 166.

Reaka, M. L., and R. B. Manning. 1987. The significance of body size, dispersal potential, and habitat for rates of morphological evolution in stomatopod Crustacea. Smithsonian Contributions

to Zoology 448.

Rogers, D. J., and T. T. Tanimoto. 1960. A computer program for classifying plants. Science 132:1115-1118.

Rowe, G. T. 1985. Benthic production and processes off Baja California, northwest Africa and Peru: A classification of benthic subsystems in upwelling ecosystems. Pp. 589-612 in Simposio Internacional sobre las Areas de Afloramiento Mas Importantes del Oeste Africano (Cabo Blanco y Benguela). Instituto de Investigaciones Pesqueras, Barcelona.

-, and R. L. Haedrich, 1979. The biota and biological processes of the continental slope. Society of Economic Palaentologists and Mineralogists Special Publication 27:49-59.

de Saint Laurent, M. 1972. Sur la famille des Parapaguridae Smith, 1882. Description de Typhlopagurus foresti gen, nov., sp. nov., et de quinze éspèces ou sous-éspèces nouvelles de Parapagurus Smith (Crustacea, Decapoda). Bijdragen Tot de Dierkunde 42:97-123.

Schmitt, W. L. 1921. The marine decapod Crustacea of California. University of California Publications in Zoology 23:1-470.

Sneath, P. A., and R. R. Sokal. 1973. Numerical Taxonomy. Freeman, San Francisco.

Takeda, M., and H. Hatanaka. 1984. Records of decapod crustaceans from the southwestern Atlantic collected by the Japanese fisheries research trawlers. Bulletin of the National Science Museum, Tokyo. Series A (Zoology), 10:7-24.

Valentine, J. W. 1966. Numerical analysis of marine molluscan ranges of the extratropical northeastern Pacific shelf. Limnology and Oceanography 11:198-211.

Wenner, E. L. 1979. Distribution and reproduction of nematocarcinid shrimp (Decapoda: Caridea) from the northwestern north Atlantic. Bulletin of Marine Science 29:380-393.

Wicksten, M. K. 1977. Range extensions of four species of crangonid shrimps from California and Baja California, with a key to the genera (Natantia: Crangonidae). Proceedings of the Biological Society of Washington 90:963-967.

1978. The species of Plesionika from California and western Mexico (Natantia: Pandalidae). Bulletin of the Southern California

Academy of Sciences 77:84-87.

1979a. New records of the species of Glyphocrangon in the northeastern Pacific Ocean (Caridea: Glyphocrangonidae). Proceedings of the Biological Society. of Washington 92:217-224.

-. 1979b. Range extensions of four species of crangonid shrimps in the eastern Pacific Ocean (Decapoda: Crangonidae). Bulletin of the Southern California Academy of Sciences 79:38-41.

1979c. Zoogeographical affinities of the broken back shrimp (Caridea: Hippolytidae) of western South America. In Proceedings of the International Symposium on Biogeography and Evolution in the Southern Hemisphere. New Zealand Department of Scientific and Industrial Research Information Series 137, Vol. 2: 627-634.

-. 1980. Mainland and insular assemblages of benthic decapod crustaceans of southern California. Pp. 357-367 in D. M. Power (ed.). The California Islands: Proceedings of a Multidisciplinary Symposium. Santa Barbara Museum of Natural History, Santa Barbara, California.

1981. New records of Stereomastis sculpta pacifica (Faxon) (Decapoda: Polychelidae) in the

- eastern Pacific Ocean. Proceedings of the Biological Society of Washington 93:914–919.
- ——. 1982a. Crustaceans from baited traps and gill nets off southern California. California Fish and Game 68:244–248.
- ——. 1982b. Two species of *Odontozona* (Decapoda: Stenopodidae) from the eastern Pacific. Journal of Crustacean Biology 2:130-135.
- ——. 1984. New records and a new species of hippolytid shrimp from the northeastern Pacific. Crustaceana 46:241–248.
- . 1987. Range extensions of offshore decapod crustaceans from California and western Mexico. California Fish and Game 73:54–56.
- -----, and M. Mendez. 1982. New records and new species of the genus *Lebbeus* (Caridea: Hippolytidae) in the eastern Pacific Ocean.

- Bulletin of the Southern California Academy of Sciences 81:106–120.
- , and ——. 1983. Bathypalaemonella delsolari, a new species of shrimp from Peru (Decapoda, Caridea, Campylonotidae). Crustaceana 45:225–231.
- ——, and ———. 1985. *Processa pippinae*: A new species of deep-sea shrimp from the Gulf of California. Crustaceana 49:16–21.
- Williams, A. B. 1986. Mud shrimps, *Upogebia*, from the eastern Pacific (Thalassinoidea: Upogebiidae). San Diego Society of Natural History Memoir 14.
- Zarenkov, N. A. 1976. K faune desyatinogikh rakoobraznykh priamerikanskikh yuzhnugo polushariya. Biologiya Morya 5:8–18.

# APPENDIX 1: SPECIES LIST OF OFFSHORE DECAPOD CRUSTACEANS OF THE EASTERN PACIFIC OCEAN

D = depth category. 1 = 0-500 m, 2 = 500-1000 m, 3 = 1000-1500 m, 4 = 1500 m and deeper. S = square (see Figs. 1-6). References for distribution are given in parentheses after depth range.

#### Suborder Dendrobranchiata

# Family Penaeidae

Benthesicymus altus Bate, 1881: San Nicolas Is., California to Galapagos, 916–4089 m (Schmitt 1921). D 3, 4; S 26. 27, 28, 29, 33, 34, 35, 37, 39, 40, 41, 42, 43, 44, 45, 46, 67, 68, 69, 70.

Benthesicymus tanneri Faxon, 1893; San Diego, California, to Peru–Chile border, 606–2422 m (Schmitt 1921, Mendez 1981). D 2, 3, 4; S 26, 27, 28, 29, 30, 31, 33, 34, 35, 37, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 67, 68, 69, 70.

Haliporoides diomedeae (Faxon, 1893); Gulf of Panama to S. Chile, 440–3455 m (Mendez 1981). D 2, 3, 4; S 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60.

Hymenopenaeus doris (Faxon, 1893); Mexico to northern Peru, 549–4802 m (Mendez 1981). D 2, 3, 4; S 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49.

Hymenopenaeus nereus (Faxon, 1893): Costa Rica to Ecuador, 330–1300 m (Mendez 1981). D 3, 4; S 42, 43, 44, 45, 46, 67, 68, 69, 70.

#### Suborder Pleocyemata

# Infraorder Stenopodidea

# Family Stenopodidae

Odontozona ?spongicola (Alcock and Anderson, 1899): off Santa Catalina Island, California, 609 m (Wicksten 1982). D 2; S 26.

Spongicoloides galapagensis Goy, 1980: Galapagos Islands, 717 m. D 2; S 69.

#### Infraorder Astacidea

# Family Nephropidae

Nephropsis occidentalis Faxon, 1893: west coast of Baja California to Chile, 550–1238 m (Manning 1970). D 2, 3; S 27, 28, 29, 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56.

# Infraorder Palinura

#### Family Polychelidae

Polycheles chilensis Sund, 1920: west of Valparaiso, Chile, 2500 m (Holthuis 1952). D 4; S 56.

Polycheles tanneri Faxon, 1893; Gulf of Panama to off Galapagos. 1079–1411 m (Faxon 1893). D 3, S 41, 42, 43, 44, 45, 68.

*Stereomastis nana* (S. Smith, 1884): cosmopolitan, 1544–2412 m (Firth and Pequegnat 1971). D 3, 4; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 62, 63, 65, 66, 67, 68, 69, 70, 71, 72.

Stereomastis sculpta pacifica (Faxon, 1893): San Clemente Island, California, to off Valparaiso, Chile; 1000–3692 m (Faxon 1893, Schmitt 1921, Wicksten 1981). D 3, 4; S 26, 27, 28, 29, 30, 31, 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56.

Stereomastis suhmi (Bate, 1878): off Valparaiso, Chile; circum-Antarctic, 293–2220 m (Firth and Pequegnat 1971). D 2, 3, 4; S 55, 56, 57, 58, 59, 60, 62, 63, 65, 66.

Willemoesia challengeri Sund, 1920: off Valparaiso, Chile, 2520–4000 m (Holthuis 1952). D 4; S 56.

Willemoesia pacifica Sund, 1920: off Valparaiso, Chile, 2520 m (Holthuis 1952). D 4; S 56.

#### Infraorder Thalassinidea

#### Family Axiidae

Axiopsis spinulicauda (Rathbun, 1902): Vancouver Island, Canada, to Bodega Head, California, 59–256 m (Hart 1982). D 1, 2; S 17, 18, 20, 23, 24.

Axius acutifrons (Bate, 1888): off San Clemente Island, California; off Mariato Point, Panama; 595–2310 m (Wicksten 1982). D 2, 3, 4; S 26, 27, 28, 29, 33, 34, 35, 36, 37, 39, 40, 41, 42.

Axius cristagalli Faxon, 1893: off Mariato Point, Panama, 852 m (Faxon 1895). D 2; S 42.

Calastacus stilirostris Faxon, 1893: southwest of Vancouver Island, Canada, to Peru, 700–1208 m (Hart 1982). D 2, 3;

S 18, 20, 23, 24, 25, 26, 27, 28, 29, 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 48.

Calocaris investigatoris (Anderson, 1896): Aleutian Islands to San Diego, California, 549–1733 m (McCauley 1972, Pereyra and Alton 1972, Hart 1982). D 2, 3; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 20, 22, 23, 24, 25, 26.

Calocaris quinqueseriatus (Rathbun, 1902): Sea of Okhotsk to Gulf of California, 288–220 m (Hart 1982). D 1, 2, 3; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 20, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 33.

Uroptychus bellus Faxon, 1893: off Mariato Point, Panama, 333-599 m (Faxon 1895). D 2; S 42.

Uroptychus nitidus occidentalis Faxon, 1893: Gulf of Panama, 839 m (Faxon 1895). D 2; S 43.

Uroptychus pubescens Faxon, 1893: off Mariato Point, Panama, 333-590 m (Faxon 1895). D 2; S 42.

#### Family Callianassidae

Callianassa goniophthalma Rathbun, 1902: Alaska to southern California, 483–651 m (Wicksten 1987). D 2; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20, 22, 23, 24, 25, 26.

# Family Upogebiidae

Upogebia jonesi Williams, 1986: northern Gulf of California to Panama, 20–74 m. D 1, S 30, 31, 32, 33, 34, 35, 36, 38, 39, 40, 41, 42, 43.

Upogebia lepta Williams, 1986: off Santa Catalina Island, California, to Islas Coronados, Mexico, 73–103 m. D 1; S 26.

# Infraorder Caridea

# Family Nematocarcinidae

Nematocarcinus agassizi Faxon, 1893: Mexico to Peru, 41–900 m (Mendez 1981). D 1, 2; S 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 51, 52.

*Nematocarcinus ensifer* Smith, 1882: Gulf of California to off Ecuador, 1218–3212 m (Wenner 1979). D 2, 3; S 31, 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45.

Nematocarcinus proximatus Bate, 1888: off Valpariaso and Valdivia, Chile, 2516–2654 m (Holthuis 1952). D 4; S 56, 58.

# Family Campylonotidae

Bathypalaemonella delsolari Wicksten and Mendez, 1983: off Peru, 712–744 m. D 2; S 48.

Campylonotus semistriatus Bate, 1888: southern Chile to Cape Horn, 30–816 m (Mendez 1981). D 1, 2; S 58, 59, 60, 61, 62, 63, 64, 65, 66.

## Family Hippolytidae

Eualus barbatus (Rathbun, 1899): Pribilof Islands to Santa Monica Bay, California, 82–507 m (Butler 1980, Wicksten 1984). D 1, 2; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 23, 24, 25, 26.

Eualus biunguis (Rathbun, 1902): Kurile Islands and Bering Sea to Oregon, 90–2090 m (Birshtein and Zarenkov 1970, Butler 1980). D 1, 2, 3, 4; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 20, 22, 23.

Eualus macrophthalmus (Rathbun, 1902): Unalaska to Point Sur, California, 110–1163 m (Butler 1980). D 1, 2, 3; S 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20, 22, 23, 24.

Eualus pusiolus (Kroyer, 1841): Bering Sea to British Columbia, 0–138 m (Butler 1980). D 1, 2, 3; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20.

Eualus suckleyi (Stimpson, 1864): Bering Sea to Washington, 11–1025 m (Birshtein and Zarenkov 1970, Butler 1980). D 1, 2, 3; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20.

*Eualus townsendi* (Rathbun, 1902): Pribilof Islands to Puget Sound, 38–630 m (Butler 1980). D 1, 2; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20.

Heptacarpus flexus (Rathbun, 1902): Bering Sea to Drake's Bay, California, 37–1189 m (Schmitt 1921). D 1, 2, 3; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20, 23, 24.

Heptacarpus moseri (Rathbun, 1902): Bering Sea to off Oregon, 108–1100 m (Butler 1980). D 1, 2, 3; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20.

Heptacarpus yaldwyni Wicksten, 1984: off Salina Cruz, Mexico, 1052-1145 m. D 3; S 37.

Lebbeus bidentatus Zarenkov, 1976: off Peru, 1680 m. D 3; S 51.

Lebbeus carinatus Zarenkov, 1976: off Peru, 1850 m. D 3; S 48.

Lebbeus curvirostris Zarenkov, 1976: off Peru, 1680–1860 m. D 3, S 48, 49, 50, 51.

Lebbeus scrippsi Wicksten and Mendez, 1982: Peru to Chile, 768–1164 m. D 2, 3; S 51, 52, 53.

Lebbeus splendidus Wicksten and Mendez, 1982: off Peru, 712-1100 m. D 2, 3; S48.

Lebbeus vicinus montereyensis Wicksten and Mendez, 1982: Monterey Bay, California, to Gulf of California, 954–2086 m. D 3, 4; S 24, 25, 26, 27, 28, 29, 33.

Lebbeus vicinus vicinus (Rathbun, 1902); north of Unalaska, 556–730 m (Rathbun 1904), D 2; S 5.

Lebbeus washingtonianus (Rathbun, 1902): Queen Charlotte Islands to off San Clemente Island, California, 820–1808 m (Butler 1980), D 3; S 16, 17, 18, 20, 23, 24, 25, 26.

Leontocaris pacificus Zarenkov, 1976; off Chile, 600-700 m. D 2, S 51.

Spirontocaris holmesi Holthuis, 1947: Yes Bay, Alaska, to San Diego, California, 24–386 m (Butler 1980). D 1, 2; S 14, 16, 17, 18, 20, 23, 24, 25, 26.

*Spirontocaris sica* Rathbun, 1902: Restoration Bay, British Columbia, to off Cedros Island, Baja California, 88–849 m (Butler 1980, Wicksten 1987). D 2, 3; S 16, 17, 18, 20, 23, 24, 25, 26, 27.

# Family Processidae

Processa pippinae Wicksten and Mendez, 1985: Gulf of California, 265-644 m. D 2, 3; S 31.

## Family Pandalidae

Heterocarpus affinis Faxon, 1893: Islas Tres Marias, Mexico, to Peru, 660–800 m (Mendez 1981). D 2; S 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49.

Heterocarpus hostilis Faxon, 1893: Gulf of Panama to Peru, 187–1000 m (Mendez 1981). D 1,2,3; S 44, 45, 46.

Heterocarpus reedi Bahamonde, 1955: off Chile, 200-500 m (Mendez 1981). D 2; S 54, 55, 56, 58.

Heterocarpus vicarius Faxon, 1893: Gulf of California to Peru, 73–800 m (Mendez 1981). D 1, 2; S 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 51.

Pandalopsis ampla Bate, 1888: Washington to Gulf of California, 553–1986 m (Schmitt 1921, Wicksten 1987). D 3; S 20, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33.

Pandalopsis dispar Rathbun, 1902: Bering Sea to Oregon, 46–649 m (Butler 1980). D 1, 2; S 1, 2, 33, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20.

*Pandalus borealis* Kroyer, 1838: Bering Sea to off Columbia River, 16–1380 m (Butler 1980). D 1, 2, 3; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 20.

Pandalus goniurus Stimpson, 1860: Bering Sea to Puget Sound, 5–450 m (Butler 1980). D 1, 2; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20.

Pandalus hypsinotus Brandt, 1851: Norton Sound, Alaska to Puget Sound, 5–460 m (Butler 1980). D 1, 2; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20.

*Pandalus jordani* Rathbun, 1902; Unalaska Island to San Nicolas Island, California, 36–457 m (Butler 1980). D 1, 2; S 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20, 23, 24, 25, 26.

Pandalus platyceros Brandt, 1851: Unalaska Island to San Diego, 0–1846 m (Butler, 1980). D 1, 2, 3; \$ 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20, 23, 24, 25, 26.

*Pandalus stenolepis* Rathbun, 1902: Unalaska Island to Hecata Bank, Oregon, 49–229 m (Butler 1980). D 1, 2; S 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20, 23.

Pandalus tridens Rathbun, 1902: Pribilof Islands to San Nicolas Island, 5–1984 m (Butler 1980). D 1, 2, 3; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 20, 22, 23, 24, 25, 26.

Plesionika beebei Chace, 1937: Gulf of California to Peru, 73–916 m (Mendez 1981). D 1, 2, 3; S 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46.

Plesionika trispinus Squires and Barragan, 1976; Colombia to Peru, 140-430 m (Mendez 1981). D 2; S 44, 45, 46, 48.

# Family Crangonidae

Argis californiensis (Rathbun, 1902): Port Hueneme, California, to Punta Banda, Baja California, 20–286 m (Wicksten 1977). D 1, 2; S 26.

Argis ovifer (Rathbun, 1902): Bering Sea to Queen Charlotte Sound, 102–673 m (Butler 1980). D 1, 2; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17.

Crangon abyssorum Rathbun, 1902; Bering Sea to Cortez Bank, California, 97–2975 m (Birshtein and Zarenkov 1970, Butler 1980). D 1, 2, 3, 4; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 20, 23, 24, 25, 26.

Crangon lomae (Schmitt, 1921): San Miguel Island to San Diego, California, 830–1182 m (Wicksten 1980). D 2, 3; S 25, 26.

*Metacrangon procax* (Faxon, 1893): Gulf of California to southern Peru, 1209–1658 m (Mendez 1981). D 3; S 31, 32, 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 51, 52.

Metacrangon variabilis (Rathbun, 1902): Bering Sea to San Nicolas Island, California, 92–1271 m (Birshtein and Zarenkov 1970, Butler 1980). D 1, 2, 3; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 20, 23, 24, 25, 26.

Paracrangon areolata Faxon, 1893; Islas Tres Marias to Peru, 1238–1246 m (Mendez 1981). D 3; S 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52.

Sclerocrangon atrox Faxon, 1893; Islas Tres Marias to Peru, 1209–1238 m (Mendez 1981). D 3; S 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52.

Pontophilus gracilis occidentalis Faxon, 1893: off San Clemente Island, California to Peru, 1789–4082 m (Faxon 1895, Zarenkov 1976, Wicksten 1977, Chace 1984). D 1, 2, 3, 4; S 26, 27, 28, 29, 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 53, 54.

# Family Glyphocrangonidae

Glyphocrangon alata Faxon, 1893: Off Acapulco, Mexico, to off Valparaiso, Chile, 600–1300 m (Wicksten 1979, Mendez 1981). D 2, 3; S 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 53, 54, 55, 56.

Glyphocrangon loricata Faxon, 1895: Galapagos Islands to Peru, 605-769 m (Mendez 1981). D 2; S 46, 48, 67, 68, 69, 70.

Glyphocrangon rimapes Bate, 1888: near Islas Juan Fernandez, 2500 m (Holthuis 1952). D 4; S 71, 72.

Glyphocrangon sicaria Faxon, 1893: Costa Rica and Gulf of Panama, 1454–3310 m (Faxon 1895, Wicksten 1979). D 3; S 41, 42, 43.

Glyphocrangon spinulosa Faxon, 1893: Cortez Basin, California, to off Mariato Point, Panama, 1218–1374 m (Faxon 1895, Wicksten 1979). D 3; S 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 39, 40, 41, 42.

Glyphocrangon vicaria Faxon, 1893: San Clemente Basin, California, to Galapagos Islands, 1374–2441 m (Faxon 1895, Wicksten 1981). D 3, 4; S 26, 27, 28, 29, 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 67, 68, 69, 70.

#### Infraorder Anomura

#### Family Diogenidae

Paguristes turgidus (Stimpson, 1857): Chukchi Sea to San Diego, 5–465 m (Hart 1982). D 1, 2, 3; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20, 23, 24, 25, 26.

# Family Paguridae

Catapagurus diomedeae Faxon, 1893: off Mariato Point, Panama, 333 m (Faxon 1895). D 3; S 42.

Pagurus aleuticus (Benedict, 1892): Japan, Bering Sea to off Eureka, California, 208–283 m (Haig and Wicksten 1975). D 1, 2; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20, 23.

Pagurus capillatus (Benedict, 1892): Bering Sea to off Santa Cruz, California, 4–1189 m (Hart 1982). D 1, 2, 3; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20, 23, 24.

Pagurus confragosus (Benedict, 1892): Alaska to off Columbia River, 55–435 m (Hart 1982). D 1, 2; S 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 20.

Pagurus cornutus (Benedict, 1892): Bering Sea to off Oregon, 160–830 m (Hart 1982). D 2; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20.

Pagurus delsolari Haig, 1974: Peru to off Valparaiso, Chile, 275-650 m. D 2; S 53, 54, 55, 56.

Pagurus forceps (A. Milne Edwards, 1836): Coquimbo, Chile, to Straits of Magellan, 660 m (Haig 1955). D 2; S 55, 56, 57, 58, 60, 62, 63, 64, 65, 66.

Pagurus imarpe Haig, 1974: Banco de Mancora and off Punta Aguja, Peru, 570–980 m. D 2; S 46.

Pagurus tanneri (Benedict, 1892): Bering Sea to off San Diego, California, 91–1372 m (Hart 1982; USNM unpubl. record). D 1, 2, 3; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20, 23, 24, 25, 26.

# Family Parapaguridae

Parapagurus abyssorum Henderson, 1888: Gulf of California to Chile, 1410–3340 m (Garth and Haig 1971). D 3, 4; S 33, 34, 35, 37, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 53, 54, 55.

Parapagurus haigae de St. Laurent, 1972: off Santa Rosa Island, California, to Gulf of California, 55–923 m (Wicksten 1987). D 2, 3; S 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43.

Parapagurus mertensii (Brandt, 1851): Kodiak Island, Alaska, to San Nicolas Island, California, 42–2012 m (Schmitt 1921). D 1, 2, 3; S 10, 11, 12, 13, 14, 16, 17, 18, 20, 23, 24, 25, 26.

Parapagurus pilosimanus benedicti de St. Laurent, 1972: Alaska to off Islas Juan Fernandez, 415–2200 m (Haig 1955, Hart 1982). D 2, 3, 4; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72.

Probeebei mirabilis Boone, 1926: Costa Rica to Peru, 1145–3995 m (Garth and Haig 1971). D 3, 4; S 41, 42, 43, 44, 45, 46, 48, 49, 50, 51.

# Family Lithodidae

Glyptolithodes cristatipes (Faxon, 1893): Palos Verdes Peninsula, California, to Chile, 183–800 m (Wicksten 1982). D 2; S 26, 27, 28, 29, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 51, 52, 53, 54, 55.

Lithodes aequispina Benedict, 1894: Bering Sea to Vancouver Island, 275–366 m (Birshtein and Zarenkov 1970, Hart 1982). D 2; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20.

Lithodes couesi Benedict, 1894: Japan and Alaska to San Diego, California, 384–1125 m (Hart 1982). D 2, 3; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 20, 23, 24, 25, 26.

Lithodes panamensis Faxon, 1893: off Panama to Peru, 760–850 m (Haig 1974). D 2; S43, 44, 45, 46, 49, 51, 52, 53. Lithodes wiracocha Haig, 1974: off Peru, 620–800 m. D 2; S 46, 48, 49.

Lopholithodes diomedeae Faxon, 1893: off Panama to Peru, 830–935 m (Haig 1974). D 2; S 43, 44, 45, 46, 48, 49, 51. Lopholithodes foraminatus (Stimpson, 1859): British Columbia to San Diego, California, 0–547 m (Hart 1982). D 1, 2, 3; S 16, 17, 18, 20, 23, 24, 25, 26.

Neolithodes diomedeae (Benedict, 1894): off Chonos Archipelago and Chiloe Island, Chile, 1923–2459 m. D 3, 4; S 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 48, 499, 50, 51, 52, 53, 54, 55, 56, 58, 59.

Paralithodes californiensis (Benedict, 1894): Monterey Bay to San Diego, California, 148–306 m (Schmitt 1921, Anderson and Cailliet 1974). D 1, 2; S 24, 25, 26.

Paralithodes rathbuni (Benedict, 1894): Cordell Bank to San Diego, California, 165-500 m (Schmitt 1921, Wicksten 1987). D 1, 2; S 24, 25, 26.

Paralomis aspera Faxon, 1893: off Panama to Peru, 560–1270 m (Haig 1974). D 2, 3; S 42, 43, 44, 45, 46.

Paralomis inca Haig, 1974: off Peru, 620-744 m. D 2; S 48, 49.

Paralomis longipes Faxon, 1893: 760-1410 m (Haig 1974). D 2, 3; S 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52.

*Paralomis multispina* (Benedict, 1894): Alaska to San Diego, California, 500–1665 m (Hart 1982). D 2,.3; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 20, 23, 24, 25, 26.

Paralomis papillata (Benedict, 1895): off Baja California, Mexico, to Peru, 712-744 m (Haig 1974). D 2; S 29, 33, 34,

35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 48,

Paralomis verrilli (Benedict, 1894): Sca of Okhotsk to Cortez Bank, California, 1238–2379 m (Hart 1982). D 3, 4; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 20, 23, 24, 25, 26.

#### Family Chirostylidae

Chirostylus defensus (Benedict, 1902); off Galapagos Islands, 214 m (Haig 1968), D 2; S 67.

Chirostylus milneedwardsi (Henderson, 1885): southern Chile to Magellanic region, 733 m (Haig 1968). D 2; S 63, 64.

Chirostylus perarmatus Haig, 1968: north of Anacapa Island, California, 229 m. D 2; S 26.

Chirostylus sp.: southwest of Vancouver Island to off Columbia River, 914–951 m (Hart 1982), D 3; S 18, 20.

Uroptychus granulatus Benedict, 1902: off Galapagos Islands, 724 m. D 2; S 67.

# Family Galatheidae

Galathea californiensis Benedict, 1902: Monterey Bay, California, to Gulf of California, 104–3998 m (Schmitt 1921, Wicksten 1987). D 1, 2, 3, 4; S 24, 25, 26, 27, 28, 29, 31, 32, 33.

Munida curvipes Benedict, 1902: off Archipelago de los Chonos, Chile, 1924 m. D 3; S 59, 60.

Munida gracilipes Faxon, 1893: Gulf of Panama, 280 m (Faxon 1895). D 2; S 43.

Munida hispida Benedict, 1902: Monterey Bay, California, to off Galapagos Islands, 165–500 m (Schmitt 1921, Wicksten 1982). D 2; S 26, 27, 28, 29, 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 67, 68, 69, 70.

Munida ?micropthalma A. Milne Edwards, 1880: off Cocos Island, 245 m (Faxon 1895). D 2; S 41.

Munida obesa Faxon, 1893: Gulf of Panama, 385 m (Faxon 1895). D 2; S 42, 43.

Munida perlata Benedict, 1902: southern Gulf of California, 3292–1920 m (Luke 1977). D 3, 4; S 33.

Munida propinqua Faxon, 1893: Gulf of Panama to Peru, 1290–1713 m (Garth and Haig 1971). D 3; S 43, 44, 45, 46, 48, 49, 51.

Munida quadrispina Benedict, 1902: Alaska to off Baja California, Mexico, 22–1463 m (Hart 1982, AHF unpubl. data). D 1, 2, 3; S 13, 14, 16, 17, 18, 20, 23, 24, 25, 26, 27, 28.

Munida refulgens Faxon, 1893: near Islas Tres Marias, Mexico, to off Isla Malpelo, Colombia, 95–183 m. D 1; S 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44.

Munidopsis aculeata Henderson, 1888: southern California to Chile, 2519–3285 m (Faxon 1895). D 4; S 26, 27, 28, 29, 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 53, 54, 55.

Munidopsis agassizi Faxon, 1893: Gulf of Panama, 385 m (Faxon 1895). D 2; S 43.

Munidopsis antoni (A. Milne Edwards, 1884): cosmopolitan, Baja California, Peru, off Islas Juan Fernandez, 2519–3676 m (Luke 1977). D 4; S 27, 28, 299, 33, 34, 35, 37, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 53, 54, 55, 56, 71, 72.

Munidopsis aries (A. Milne Edwards, 1880); off Oregon, 2850 m (Ambler 1980). D 4; S 22.

*Munidopsis aspera* (Henderson, 1885): Santa Catalina Island, California, to Straits of Magellan, 104–2748 m (Haig 1955). D 1, 2, 3, 4; S 26, 27, 28, 29, 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 53, 54, 56, 58, 59, 60, 62, 63, 64, 65, 66.

Munidopsis bairdii (Smith, 1884): Oregon to Panama, cosmoplitan, 1920–3292 m (Ambler 1980). D 3, 4; S 22, 24, 25, 26, 27, 28, 29, 33, 34, 35, 37, 39, 40, 41, 42, 43.

Munidopsis beringana Benedict, 1902: Bering Sea to Oregon, 2800–3276 m (Ambler 1980). D 4; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 15, 16, 17, 18.

Munidopsis carinipes Faxon, 1893: off Mariato Point, Panama, 1273 m (Faxon 1895). D 3; S 42.

Munidopsis cascadia Ambler, 1980: Cascadia Basin, off Oregon, 2743-2926 m. D 4; S 18, 22.

Munidopsis ciliata Wood-Mason, 1891: Oregon to Panama, 2030–2875 m (Ambler 1980). D 4; S 18, 22, 24, 25, 26, 27, 28, 29, 33, 34, 35, 37, 39, 40, 41, 42, 43.

Munidopsis crinita Faxon, 1893: Gulf of Panama, 839 m (Faxon 1895). D 2; S 43.

Munidopsis depressa Faxon, 1893: Santa Catalina Island, California, to off Islas Tres Marias, Mexico, 185–1255 m (Haig 1955). D 1, 2, 3, 4; S 26, 27, 28, 29, 33.

Munidopsis diomedae (Faxon, 1893): San Clemente Island, California, to Chile, 768–3790 m (Haig and Wicksten 1975, Luke 1977). D 2, 3, 4; S 26, 27, 28, 29, 33, 34, 35, 37, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 53.

Munidopsis hamata Faxon, 1893: off Baja California and Gulf of Panama, 936–1337 m (Faxon 1895, Luke 1977). D 3; S 29, 43.

Munidopsis hendersoniana Faxon, 1893; Gulf of Panama, 1869 m (Faxon 1895). D 3; S 43.

Munidopsis hystrix Faxon, 1893; Anacapa Island, California, to Peru, 552–1243 m (Garth and Haig 1971). D 2, 3; S 26, 27, 28, 29, 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51.

Munidopsis inermis Faxon, 1893: off Mariato Point, Panama, 590 m (Faxon 1895). D 2; S 42.

*Munidopsis latirostris* (Henderson, 1895): Cascadia Plain, off Oregon, to off Panama, 280–3243 m (Ambler 1980). D 2, 3, 4; S 22, 24, 25, 26, 27, 28, 29, 33, 34, 35, 37, 39, 40, 41, 42, 44.

Munidopsis margarita Faxon, 1893: off Galapagos Islands, 705 m (Faxon 1895). D 2; S 69.

Munidopsis opalescens Benedict, 1902: southern Chile, 638-823 m (Haig 1955). D 2; S 63, 64.

Munidopsis ornata Faxon, 1893: off Galapagos Islands, 705 m (Faxon 1895). D 2; S 68.

*Munidopsis quadrata* Faxon, 1893; Queen Charlotte Islands, Canada, to off Islas Tres Marias, Mexico, 245–1574 m (Hart 1982). D 2, 3; S 16, 17, 18, 20, 23, 24, 25, 26, 27, 28, 29, 33.

Munidopsis rostrata (A. Milne Edwards, 1880): off Acapulco, Mexico, to off Galapagos Islands, 2153–2492 m (Faxon 1895). D 4; S 67, 68, 69, 70.

*Munidopsis scabra* Faxon, 1893; off Oregon to Peru, 567–1243 m (Pereyra and Alton 1972, Haig and Wicksten 1975). D 2, 3; S 22, 23, 24, 25, 26, 27, 28, 29, 33, 34, 35, 37, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 51.

Munidopsis sericea Faxon, 1893; Gulf of Panama, 936 m (Faxon 1895). D 3; S 43.

Munidopsis subsquamosa Henderson, 1885: off Oregon to off Chile, 1097–3000 m (Luke 1977, Ambler 1980). D 3, 4;

S 22, 24, 25, 26, 27, 28, 29, 33, 34, 35, 37, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 53. *Munidopsis tanneri* Faxon, 1893; Gulf of Panama, 156–415 m (Faxon 1895). D 1, 2; S 43.

Munidopsis trifida Henderson, 1885; southern Chile, 638–823 m (Haig 1955). D 2; S 63, 64.

Munidopsis tuftsi Ambler, 1980: Tufts Abyssal Plain, northern Pacific, 3500-3858 m. D 4; S 18, 19, 21, 22.

Munidopsis verrilli Benedict, 1902: off Oregon to off Cedros Island, Baja California, Mexico, 1253–1986 m (Schmitt 1921, McCauley 1972). D 3; S 18, 20, 22, 23, 24, 25, 26, 27.

Munidopsis verrucosus Khodkina, 1973: Oregon to off Antofagasta, Chile, 3932–4880 m (Ambler 1980). D 4; S 18, 19, 21, 22, 24, 25, 26, 27, 28, 29, 33, 34, 35, 37, 39, 40, 41, 42, 44, 46, 48, 50, 51, 52, 53, 54.

Munidopsis vicina Faxon, 1893: Gulf of Panama and off Cocos Island, 3063-3885 m (Faxon 1895). D 4; S 42.

Munidopsis villosa Faxon, 1893: Gulf of Panama and off Arica, Chile, 936–1773 m (Faxon 1895, Luke 1977). D 3; S 44, 53.

Munidopsis yaquinensis Ambler, 1980: off Oregon, 2763-2377 m. D 4; S 18, 19, 21, 22.

## Infraorder Brachyura

Family Homolodromiidae

Homolodromia robertsi Garth, 1973: off Peru, 800 m. D 2; S 46, 48.

Family Calappidae

Acanthocarpus delsolari Garth, 1973: off Peru, 250 m. D 1; S 46.

# Family Dorippidae

Ethusa ciliatifrons Faxon, 1893: Gulf of Panama, 280-475 m (Faxon 1895). D 1, 2; S 43.

Ethusa lata Rathbun, 1893: off Cocos Island, 183 m (Faxon 1895). D 1; S 41.

Ethusina faxonii Rathbun, 1933: western Mexico to Peru, 2999–4081 m (Garth and Haig 1971). D 3; S 36, 37. 39, 40, 41, 42, 44, 46, 48.

Ethusina robusta (Miers, 1886): Bay of Panama to Galapagos Islands and Ecuador, 1618–3334 m (Garth and Haig 1971). D 3, 4; S 42, 44, 46, 48, 65, 67, 69, 70.

Ethusina smithiana Faxon, 1893: off Cocos and Malpelo Islands, 245-1647 m (Faxon 1895). D 2, 3; S 41, 42, 44.

#### Family Cymonomidae

Cymonomus menziesi Garth, 1971: Peru, 1005-1124 m (Garth and Haig 1971). D 3; S 48.

#### Family Majidae

Chionoecetes angulatus angulatus Rathbun, 1924: Bering Sea to Oregon, 90–3330 m (Garth 1958, Birshtein and Zarenkov 1970, Hart 1982). D 1, 2, 3, 4; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20.

*Chionoecetes bairdi* Rathbun, 1924: Bering Sea to Oregon, 6–475 m (Garth 1958, Hart 1982). D 1, 2; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20.

*Chionoecetes tanneri* Rathbun, 1893: E of Kamchatka to Cortez Bank, California, 29–1944 m (Garth 1958, Hart 1982). D 1, 2, 3, 4; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 20, 23, 24, 25, 26.

*Chorilia longipes* Dana, 1851: Alaska to Cortez Bank, California, 22–1190 m (Garth 1958, Hart 1982). D 1, 2, 3; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20, 23, 24, 25, 26.

Chorilia longipes turgida Rathbun, 1924: Oregon to off San Diego, California, 66–1169 m (Garth 1958). D 1, 2, 3; S 20, 23, 24, 25, 26.

Hyas lyratus Dana, 1851: Bering Sea to Puget Sound, 9–640 m (Garth 1958, Hart 1982). D 1, 2; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20.

Lophorochinia parabranchia Garth, 1969: northern Peru to off Valparaiso, Chile, 128–509 m (Garth and Haig 1971). D 1, 2; S 51, 52, 53, 54.

*Oregonia bifurca* Rathbun, 1902: Bering Sea to off Columbia River, Oregon, 494–1463 m (Garth 1958, Hart 1982). D 2, 3; S 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 20.

Rochinia cornuta (Rathbun, 1898): off Galapagos Islands, 718-1160 m (Garth 1958). D 2, 3; S 69.

Rochinia occidentalis (Faxon, 1893): off Galapagos Islands, 705 m (Garth 1958). D 2; S 69.

## Family Atelecyclidae

Trachycarcinus corallinus Faxon, 1893: off Acapulco, Mexico, to Peru, 834–1280 m (Garth and Haig 1971). D 2, 3; S 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 48.

*Trachycarcinus hystricosus* Garth, 1971: Peru to Chile, 907–935 m (Garth and Haig 1971). D 1, 2, 3; S 46, 48, 49, 50, 51, 52, 53, 54, 55, 56.

### Family Palicidae

Cympolia tuberculata Faxon, 1893: Bay of Panama, 333 m (Rathbun 1918). D 2; S 42.

#### Family Goneplacidae

Trizocarcinus peruvianus Garth, 1973: off Paita, Peru, 144 m (Garth 1973). D 1, S 48.